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Understanding the effects of climate change via disturbance on pristine arctic lakes—multitrophic level response and recovery to a 12-yr, low-level fertilization experiment

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Abstract

Effects of climate change-driven disturbance on lake ecosystems can be subtle; indirect effects include increased nutrient loading that could impact ecosystem function. We designed a low-level fertilization experiment to mimic persistent, climate change-driven disturbances (deeper thaw, greater weathering, or thermokarst failure) delivering nutrients to arctic lakes. We measured responses of pelagic trophic levels over 12 yr in a fertilized deep lake with fish and a shallow fishless lake, compared to paired reference lakes, and monitored recovery for 6 yr. Relative to prefertilization in the deep lake, we observed a maximum pelagic response in chl *a* (+201%), dissolved oxygen (DO, −43%), and zooplankton biomass (+88%) during the fertilization period (2001–2012). Other responses to fertilization, such as water transparency and fish relative abundance, were delayed, but both ultimately declined. Phyto- and zooplankton biomass and community composition shifted with fertilization. The effects of fertilization were less pronounced in the paired shallow lakes, because of a natural thermokarst failure likely impacting the reference lake. In the deep lake there was (a) moderate resistance to change in ecosystem functions at all trophic levels, (b) eventual responses were often nonlinear, and (c) postfertilization recovery (return) times were most rapid at the base of the food web (2–4 yr) while higher trophic levels failed to recover after 6 yr. The timing and magnitude of responses to fertilization in these arctic lakes were similar to responses in other lakes, suggesting indirect effects of climate change that modify nutrient inputs may affect many lakes in the future.

Introduction

Lakes are sensitive to the effects of climate change (Adrian et al. 2009; Schindler 2009). Climate change influences lake ecosystems via warmer waters (e.g., Baulch et al. 2005; Schneider and Hook 2010), timing of ice-on and ice-off (Caldwell et al. 2020), and changes to thermal structure (e.g., thickness of the epilimnion; Kraemer et al. 2015). However, warmer air temperatures will not necessarily translate solely to warmer lake habitat (Keller 2007). Other indirect effects of warmer temperatures on lake ecosystems can be subtle and include changes in lake and stream chemistry due to increased weathering in the catchment (Hobbie et al. 2017; Kendrick et al. 2018) and both decreased (Schindler 2009) and increased nutrient loading (e.g., Christoffersen et al. 2008). These indirect effects of climate change may emerge slowly, and thus require long-term studies to detect, but may be as or more influential on lake ecosystem processes than the direct effects of warming (e.g., Hobbie et al. 2017).

The climate is changing faster in the Arctic than any place on earth (IPCC 2014; Overland et al. 2015; Box et al. 2019). As a result, there are direct effects of climate change to lakes such as increased water temperature, and indirect effects that

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occur in response to increased air temperatures (Adrian et al. 2009; Schindler 2009; Hobbie and Kling 2014). These indirect effects of climate change include increases in the frequency and magnitude of disturbances such as tundra fires (Hu et al. 2010, 2015; Mack et al. 2011) and land-surface failures due to melting ground ice (termed thermokarst failures), which can persist in some instances long enough to be considered a significant, press disturbance (Bowden et al. 2008; Schuur et al. 2009; 2014). Both types of disturbance result in the mass transport of soil (e.g., sediment, carbon), vegetation, and dissolved constituents (nutrients) into surface waters, with the potential to dramatically alter aquatic ecosystem function and biological interactions over relatively shorter (e.g., fire) and longer (e.g., thermokarst, weathering) temporal scales (Mack et al. 2011; Luecke et al. 2014; Hobbie et al. 2017; Kendrick et al. 2018). The sediment and nutrients delivered to aquatic ecosystems after these disturbances likely have a variety of effects, including reduction in water clarity and associated changes in lake processes determined in part by light attenuation and increased productivity at multiple trophic levels due to increased nutrient availability (Evans 2007; Luecke et al. 2014; Gough et al. 2016). Ultimately, these changes to aquatic ecosystems result in long-term shifts in population and community structure at upper trophic levels (Slavik et al. 2004; Budy and Luecke 2014; Gough et al. 2016).

The Arctic has thousands of lakes that are relatively free of local anthropogenic disturbances (Hobbie and Kling 2014) and demonstrate considerable variation in morphometry, biogeochemistry, and composition of biotic communities (Kling et al. 1992; Hershey et al. 1999; Luecke et al. 2014). Nonetheless, there are consistencies across arctic lakes that include generally low productivity (oligotrophic to ultra-oligotrophic), low species diversity, and a limited time period of concentrated biological activity at upper trophic levels over the short but intense (~24 h of daylight) ice-free season (Vincent and Hobbie 2000; Christoffersen et al. 2008; Kling 2009). Due to these characteristics, arctic lakes may be particularly sensitive to changes in nutrient delivery as a result of climate-driven disturbances (Hobbie et al. 1999; Hobbie and Kling 2014; Gough et al. 2016). In contrast, however, the relatively simple food webs of arctic lakes, strong temperature limitation, and relatively low invisibility suggest that arctic lakes might be resistant to disturbance (i.e., limited state spaces; Carpenter et al. 2001). Furthermore, it remains to be determined how arctic lakes will respond differently to disturbance based on variation in physical and biogeochemical characteristics among lakes.

Increased nutrient loading in arctic lakes can follow and stimulate several different trophic pathways, which vary depending on lake size, morphometry, and complexity of the food web (Luecke et al. 2014; Klobucar et al. 2018; Klobucar and Budy 2020). Because benthic primary production is more likely to be light limited than nutrient limited, the response of primary producers to nutrient addition might differ in shallow lakes, which are dominated by benthic primary production, than in deep lakes where phytoplankton production dominates (Vadeboncoeur et al. 2001, 2003; Karlsson et al. 2009). We also might expect the positive response by zooplankton to fertilization to be stronger in lakes without fish compared to lakes with fish, because fish can dramatically reduce zooplankton standing stock, diversity, and size (Brooks and Dodson 1965; Carpenter and Kitchell 1996; Johnson et al. 2010). Some potential effects of increased nutrient loading on arctic lakes were evaluated previously in relatively short-term, high-level fertilization bioassays, mesocosms, and whole-lake fertilization studies associated with the Arctic Long-Term Ecological Research program (ARC LTER; Luecke et al. 2014). However, those "sledgehammer" manipulations (*sensu* Carpenter 1996) (1) resulted in substantial physiochemical responses and biological changes at some, but not necessarily at all trophic levels, (2) did not consider lake morphometry and fish presence explicitly, and (3) were outside the range of natural nutrient loading rates. Thus, there remains a need to understand whole-lake responses to lower-level, sustained nutrient loading that mimics what might occur with increases in climate change-induced disturbance events, such as increased weathering or thermokarst failure.

This study determined the indirect effects of climate change on arctic lake ecosystems, specifically from a persistent, low-level increase in nutrients as predicted to result from catchment changes such as permafrost thaw (Hobbie et al. 1999) or thermokarst failure. We fertilized lakes at 2–3 times the average natural annual loading rate, based on interannual variation in background nutrient loading (Daniels et al. 2015), for 12 yr, and followed recovery for 6 yr. We hypothesized the presence of fish and lake morphometry would affect differences in lake response to fertilization, because these two factors are critical to lake ecosystem function in the Arctic (Hershey et al. 1999; Vadeboncoeur et al. 2001; Luecke et al. 2014). For example, shallow lakes (<6 m deep) have no fish in the Alaskan Artic because they freeze solid over the winter, and thus we expected to see a strong positive response of zooplankton to fertilization. Deep lakes do contain fish, which we expected to respond to increased productivity but also to dampen the potential zooplankton response to increased productivity. Thus, in this study, we used treatment–reference pairs of deep and shallow lakes with and without fish. We also hypothesized that the response at lower trophic levels would be rapid given the oligotrophic state of these lakes, but that the response to fertilization would be slower (i.e., lagged) at higher trophic levels given their longer generation times. Similarly, we predicted the return time of recovery would be more rapid at lower trophic levels and slower at higher trophic levels.

Methods

The study occurred in experimental lakes near the Toolik Field Station (TFS; 68°37′ N, 149°36′ W; http://toolik.alaska.edu/), in the primary study area of the National Science Foundation's ARC LTER program. All experimental lakes are part of the ARC

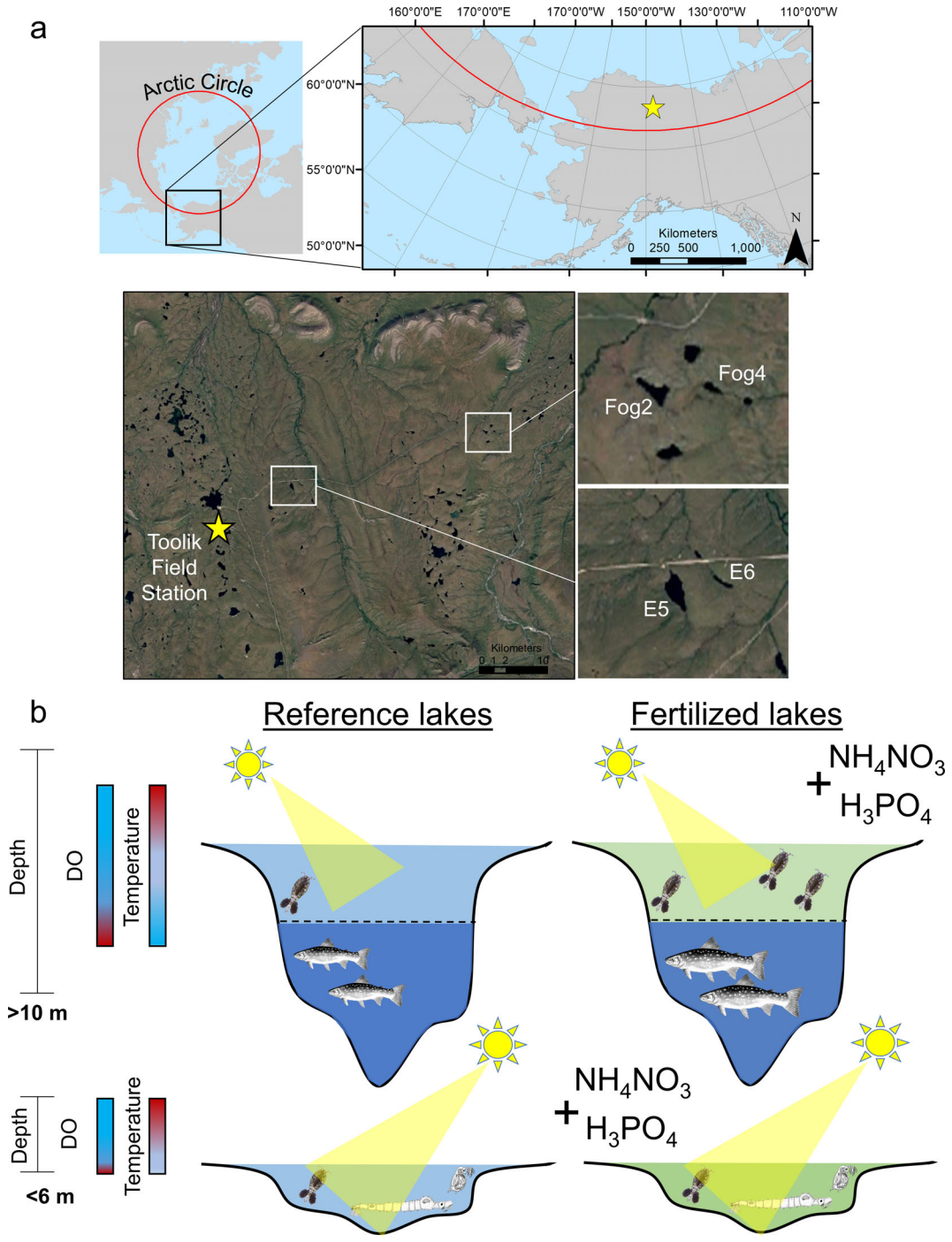

Figure 1. (**a**) Location of Toolik Field Station (star) located on the North Slope of the Brooks Mountain Range, Alaska. The four lakes included in the experiment are labeled: E5 = fertilized deep lake with fish, E6 = fertilized shallow lake without fish, Fog 2 = reference deep lake with fish, Fog 4 = reference shallow lake without fish. (**b**) Conceptual diagram representing the two pairs of deep and shallow lakes. We manipulated one lake of each pair by fertilizing it with N and P, while keeping the other lake as a reference. Deep lakes typically stratify (dashed horizontal line) in the summer and contain fish. Sunlight reaches the bottom of the shallow lakes and these lakes are well mixed by wind. Zooplanktons are more numerous in the shallow lakes where fish are absent. We expected nutrient additions would stimulate primary producers (green shading), and zooplankton would increase in response. In the fertilized deep lake we expected fish condition would increase with food availability.

LTER monitoring program (https://arc-lter.ecosystems.mbl.edu/). The TFS is located on the North Slope of the Brooks range in Alaska, U.S.A. (Figure 1a). Study lakes are surrounded by permafrost soils with summer soil active (thawed) layers less than 1 m thick; mean annual air temperature is −7°C, and mean July temperature is 12°C (Hobbie and Kling 2014).

Table 1. Prefertilization lake characteristics from (https://arc-lter.ecosystems.mbl.edu) and limnological characteristics from Luecke et al. (2014). Metrics for limnological characteristics are the mean for samples collected from epilimnetic water (0–3 m) in July of each year, 1999–2008 (prefertilization).

Lake name	Lake type	Elevation (m)	Area (ha)	Max depth (m)	Volume (m^3)	Secchi (m)	TN (μM)	TP (μM)	Chl *a* ($\mu g\ L^{-1}$)
E5	Fertilized deep lake w/fish	800	11.3	12.7	703,376	3.6	18.35	0.31	1.22
Fog 2	Reference deep lake w/fish	792	3.7	20.3	469,114	8.4	11.72	0.14	0.71
E6	Fertilized shallow, fishless	796	2.0	3.2	34,819	2.2	20.57	0.42	1.83
Fog 4	Reference shallow, fishless	754	2.3	5.4	42,991	2.2	24.29	0.44	3.59

Although quite variable (by up to 3 weeks), the lakes are generally ice free from mid-June to late-September.

We used a two-factor study design including fertilized and reference (no fertilization) deep lakes with fish and shallow fishless lakes (Table 1; lake characteristics). Deep lakes with fish have a maximum depth of 12–20 m, a surface area of 6–11 ha, and are thermally stratified in summer (Figure 1b). Shallow fishless lakes have a maximum depth of 3–5 m, a surface area of ~2 ha, and are frequently mixed. All lakes used in the experiment were oligotrophic at the beginning of the experiment with mean annual summer chlorophyll *a* (chl *a*) <2 $\mu g\ L^{-1}$ (Kling et al. 1992). Arctic char (*Salvelinus alpinus*) and slimy sculpin (*Cottus cognatus*) are the only fishes present in the deep lakes, and both deep lakes are effectively closed to immigration and emigration. After 1 yr of observation, one of each pair (deep, shallow) of lakes was fertilized for 12 yr, and the other of each pair was used as a reference. Although our experimental design included keeping one lake from each pair as a reference, we observed a small, natural thermokarst event in the shallow reference lake (Fog4) near the start of the experiment (2002–2004) that likely explains some of the patterns we observed below (see also Discussion).

Nutrients were added from 2001 to 2012, and lakes were monitored annually at all trophic levels. Phytoplankton is generally co-limited by both nitrogen (N) and phosphorous (P) in these lakes (Levine and Whalen 2001). Thus, fertilizer was added in the form of ammonium nitrate (N) and phosphoric acid (P) at 2–3 times the natural loading of the lakes ($N = 56$ mg N m^{-3} yr^{-1}; $P = 8$ mg P m^{-3} yr^{-1}; Redfield Ratio; Daniels et al. 2015). Fertilizer was added continuously from early June to late August by slowly dripping liquid solution into the lakes from a raft tethered near the center of the lake.

Field sampling and laboratory analyses

We measured limnological variables at all four lakes throughout the summer of each year (15 June to 15 August) at differing intervals (by variable; Table S1) using standard limnological techniques (e.g., Wetzel and Likens 2000; *additional sampling and analysis details are available in* Kling et al. 1992, 2000; Luecke et al. 2014). Here, we report on the time series of summer pelagic data for dissolved oxygen, water transparency, chl *a* (as an index of primary production), phytoplankton, zooplankton (July only), and fish. Benthic primary production and respiration were measured in most years as part of an intensive partner study and are reported in Daniels et al. (2015).

Sampling and measurements were performed at the deepest area of the lake. We used chl *a* ($\mu g\ L^{-1}$) as an index of phytoplankton biomass; the response of primary production (mg C m^{-3} day^{-1}) is reported elsewhere (Evans 2007). We measured chl *a* fluorometrically after extraction in acetone (Axler and Owen 1994). In addition, we sampled phytoplankton taxonomic composition and biovolume using a tube sampler (8 m × 12.7 mm tygon tubing) of epilimnetic water, and had samples analyzed in 1999, 2000, 2002, 2003, 2012, and 2017 for lakes E5 and E6 and in 2002 and 2012 for lakes Fog2 and Fog4. Phytoplankton samples were analyzed by PhycoTech and BSA Environmental Services and are reported as proportional biovolume. We measured water transparency with a 200 mm standard Secchi disk.

We collected zooplankton via vertical tow (from ~1 m above the sediment to surface) with a 243 μm mesh zooplankton net. We collected samples in duplicate, preserved with sugar-buffered Lugol's solution, and identified zooplankton to species in the laboratory (Wetzel and Likens 2000). We measured zooplankton lengths under a microscope on the first 20 (if available) individuals encountered in the sample and converted lengths to dry biomass using standard length-to-mass equations from the literature (Edmondson 1974) except for *Holopedium*, which we measured, dried, and developed our own relationship: $\text{Mass}\,(\mu g) = \text{length}^{2.44 \times 11.44}$.

We then converted density estimates by species (individuals L^{-1}) to biomass by species ($\mu g\ L^{-1}$). We measured dissolved oxygen (DO; mg L^{-1}) in vertical depth profiles with a DO probe. From 2001 to 2005, we made DO measurements with a Clarkson cell probe, and from 2006 to 2019 we made measurements with an optical probe. We constructed a filled contour plot to visualize DO at depth across time for each lake using predicted values from models with DO as a response variable and the interaction between depth and year as predictor variables. We modeled the relationship between depth and year on DO using natural cubic splines (R Core Team 2019).

We sampled fish (Arctic char) populations annually using under-ice and summer angling, short-set gill nets, and fyke nets. All fish greater than 150 mm (total length; TL) were

tagged with passive integrated transponder PIT tags (Biomark, Boise, Idaho), and all fish greater than 100 mm were weighed (g) and measured (TL). Additional details of fish sampling and analyses are provided in Budy and Luecke (2014).

Statistical analyses

For all analyses unless otherwise noted, we averaged across samples collected throughout the summer to obtain a single value for each year (Table S1). For chl *a*, we averaged data from 0 to 3 m for the deep lakes, and the entire water column for the shallow lakes. We averaged zooplankton biomass (July only) across duplicates within each lake and summed across taxa to calculate total zooplankton biomass. To assess trends in DO over time, we report values from depths of 2 m for the shallow lakes and 8 m for the deep lakes. Although using annual averages likely further reduces statistical power to detect differences over the nearly 20 yr study period, this dataset represents a relatively long time period as experimental ecological data are concerned, and the observed effects were statistically quite large (see Results). All analyses were conducted with the R statistical language, version 3.5.3 (R Core Team 2019).

Whole-lake responses over time

We used generalized additive models (GAM) to quantify trends in limnological variables over time among reference and treatment lakes. A GAM is similar to a generalized linear model except with a relaxed assumption of linearity (Hastie and Tibshirani 1990; Guisan et al. 2002). A GAM uses a link function to establish a relationship between the expected value of the response variable and a function of explanatory variables that capture potential nonlinear, but smooth, relationships between predictor variables and a response variable. We fit separate models for each pair of lakes (i.e., deep lakes with fish and shallow lakes without fish) using lake and year as predictor variables. Because we were interested in testing whether trends over time differed ($\alpha = 0.05$) between fertilized and reference lakes in each pair (i.e., deep and shallow lakes), we treated lakes as ordered factors and used the "by" argument to fit smooths by lake (Pedersen et al. 2019). We included lake as a parametric predictor to account for mean differences in response variables between lakes, a smoothing term of year, and a smoothing term of year by lake. By treating lake as an ordered factor, we could statistically test for a difference of smooths between our reference and fertilized lakes. For example, the smoothing term of year estimates the relationship between a response variable and time for the reference lake, while the smoothing term of year by lake estimates if there is a difference between smooths over time between the paired reference and fertilized lakes. We fit GAM models with the mgcv package in R using restricted maximum likelihood, the default settings for smooth class (i.e., thin plate regression splines), and assumed a Tweedie distribution (Wood 2017; R Core Team 2019). We checked model assumptions using residual plots, including for autocorrelation, and observed no obvious patterns.

Phytoplankton assemblage composition

Sampling for phytoplankton composition was not consistent across treatment and reference lakes over time, which prevented us from formally testing differences in composition among lakes. Rather, we plotted proportional phytoplankton biovolume in each lake to visualize changes over time. We calculated Morisita-Horn distance among all possible pairs of samples, and then used a nonmetric multidimensional scaling ordination to visualize shifts in phytoplankton composition over time in deep and shallow lakes. We used the vegan package to conduct ordination analysis (Oksanen et al. 2019). Proportional biovolume data are available in Table S2.

Zooplankton assemblage composition

Zooplankton assemblages were sampled consistently over time from the four lakes, and to test for differences in composition over time and between fertilized and reference lakes, we used multivariate linear models (Wang et al. 2012, 2019). Using the manylm function in the mvabund package, we fit individual linear models to each species using the same set of predictor variables. (Wang et al. 2019). The *F*-statistics from each model are summed together (i.e., *Sum of F*), and this is used to test for an assemblage-level effect with a *p*-value estimated via resampling (Wang et al. 2012). The significance of individual species models is determined using permutation-based ANOVA with *p*-values corrected for multiple testing. The contribution of each species to the assemblage-level response is calculated by dividing the *F*-statistic of species-specific models by the *Sum of F*, which is similar to a SIMPER procedure used with distance-based methods (Clarke 1993; Wang et al. 2012). We used biomass of each taxa as response variables, and data were log-transformed + 1 to improve normality. We ran separate models for pairs of deep and shallow lakes.

Fish abundance and condition

Arctic char populations in these lakes are small with slow recruitment, and fish are sensitive to handling. As such, we minimized our sampling and handling as much as possible, which resulted in low fish capture and recapture rates. Consequently, data were too sparse to estimate abundance using traditional mark-recapture techniques. Thus, to quantify trends in fish abundance in the two deep lakes, we transformed catch data into catch per unit effort (CPUE), which is commonly used as an index of abundance. We also tested for differences in fish condition over time. To estimate fish condition, we calculated relative condition (K_n) as

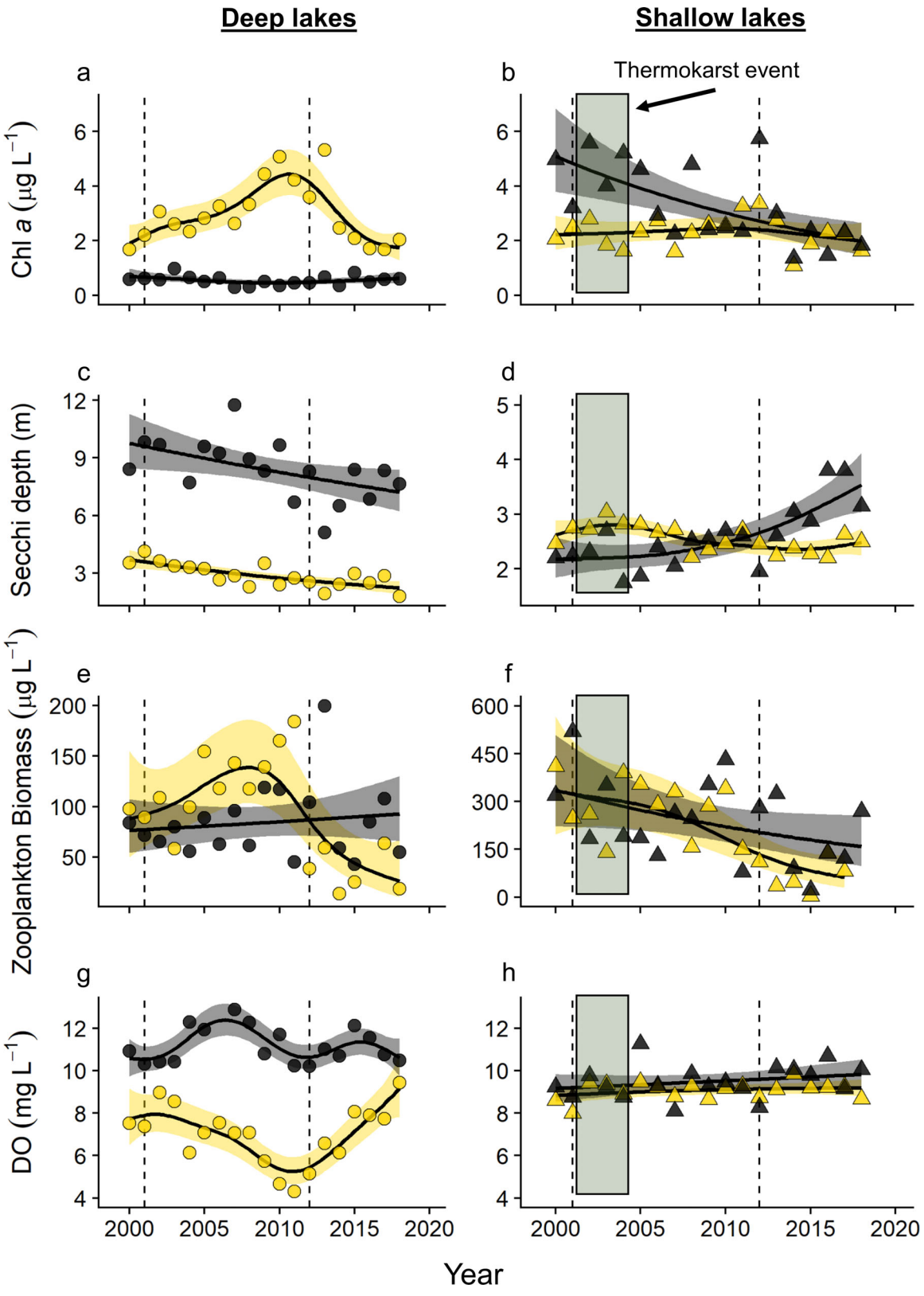

Figure 2. Epilimnetic chlorophyll a (panels **a**,**b**), water transparency (measured as Secchi depth) (panels **c**,**d**), zooplankton biomass (panels **e**,**f**), and hypolimnetic dissolved oxygen measured at 8 m (panel **g**) and 2 m (panel **h**). Deep lakes are on the left (circles) and shallow lakes are on the right (triangles). Fertilized lakes are shown in yellow symbols, and reference lakes are in black symbols. The dashed vertical lines indicate the start and end of the fertilization treatment, and the shaded boxes in the right panels represent a natural thermokarst event we observed in the shallow, reference lake. Trend Lines are smoothing splines with 95% confidence interval shading from generalized additive models. Some *y*-axis scales differ among panels. Note chlorophyll a from 2000 to 2003 represents total values uncorrected for phaeophytin.

$$K_n = \left(\frac{W}{W'}\right) \times 100$$

where W is the weight of an individual fish and W' is the predicted length-specific weight based on $\log_{10}$ transformed data. We used all fish length and weight data from both lakes to build a model to predict length-specific weight. A fish considered to be in average condition would have a value of 100. We used GAMs as described above to test for differences in CPUE, total length, and relative condition of char over time in the two lakes.

Results

Whole-lake responses over time

Temporal patterns in whole-lake responses differed between deep lakes with fish and shallow lakes without fish and based on fertilization treatment (Figure 2). The deep fertilized lake demonstrated significantly higher average chl *a* than the reference lake ($F = 435.4$, $p < 0.001$; Table 2). While chl *a* in the reference deep lake had no statistically significant trend over time, remaining below 1.0 μg L^{-1} ($F = 1.32$, $p = 0.286$; Figure 2a), in the fertilized deep lake chl *a* increased on average 201% to a max of 5.1 μg L^{-1} between 2000 and 2012, and declined after fertilization ended.

We observed a natural thermokarst failure from 2002 to 2004 in the reference shallow lake, which confounded our statistical comparison between the shallow lakes. This thermokarst appeared to deliver nutrients to the shallow reference lake and stimulate chl *a*, although there was high interannual variation. However, this event also allowed us to measure the shallow lake response to thermokarst directly and compare that to our attempt to mimic this disturbance experimentally. In the shallow lakes, average chl *a* concentration was higher in the

Table 2. Model output from generalized additive models (GAM) for limnological variables measured in four lakes in arctic Alaska. Models were run separately for deep lakes (E5 and Fog2) and shallow lakes (E6 and Fog4). Lake was included as a parametric predictor to account for differences in mean values between lakes, and we treated lakes as ordered factors to test for differences in smoothing terms between paired lakes. Positive coefficient estimates mean the reference lake had higher values, on average. We used thin plate regression splines by lake to test for differences between smoothing functions of paired lakes. *F*-statistics and effective degrees of freedom (edf) are provided, and *p*-values <0.05 are in bold. The "Reference smooth" effect represents the smoothing term for the reference lake over time, while the "Fertilized vs. reference smooth" effect represents whether smoothing splines differ between the reference and fertilized lake in a pair.

Response	Lakes	Effects	Coefficient estimate (SE)	*F*	*Edf*	*p*	Deviance explained (%)
Chl *a*	E5, Fog2	Lake	−1.66 (0.08)	435.4	1.00	**<0.001**	94.3
		Reference smooth		1.32	2.41	0.286	
		Fertilized vs. reference smooth		6.12	4.42	**<0.001**	
	E6, Fog4	Lake	0.33 (0.10)	11.05	1.00	**0.002**	47.4
		Reference smooth		8.67	1.45	**<0.001**	
		Fertilized vs. reference smooth		7.18	1.00	**0.011**	
Secchi depth	E5, Fog2	Lake	1.09 (0.05)	425.7	1.00	**<0.001**	92.7
		Reference smooth		6.09	1.00	**0.019**	
		Fertilized vs. reference smooth		1.19	1.01	0.284	
	E6, Fog4	Lake	<0.01 (0.04)	0.01	1.00	0.933	55.9
		Reference smooth		13.76	2.09	**<0.001**	
		Fertilized vs. reference smooth		28.91	1.00	**<0.001**	
Zooplankton biomass	E5, Fog2	Lake	0.01 (0.14)	0.01	1.00	0.932	44.7
		Reference smooth		0.26	1.43	0.654	
		Fertilized vs. reference smooth		3.97	3.04	**0.011**	
	E6, Fog4	Lake	0.27 (0.18)	2.38	1.00	0.132	37.4
		Reference smooth		3.84	1.00	0.059	
		Fertilized vs. reference smooth		1.91	1.90	0.167	
Dissolved oxygen (DO)	E5, Fog2	Lake	0.48 (0.03)	304.9	1.00	**<0.001**	93.5
		Reference smooth		1.48	3.90	0.213	
		Fertilized vs. reference smooth		7.11	4.96	**<0.001**	
	E6, Fog4	Lake	0.05 (0.02)	4.63	1.00	**0.039**	17.5
		Reference smooth		1.94	1.00	0.173	
		Fertilized vs. reference smooth		0.19	1.00	0.669	

reference lake ($F = 11.05$, $p = 0.002$; Table 2). Patterns of chl *a* in the shallow lakes differed significantly over time ($F = 7.18$, $p = 0.011$; Figure 2b); chl *a* in the reference lake declined over time ($F = 8.67$, $p < 0.001$), but remained relatively unchanged in the fertilized lake.

Water transparency, measured as Secchi depth, was nearly 3× higher in the reference deep lake ($F = 425.7$, $p < 0.001$; Figure 2c). Water transparency declined over time in both deep lakes ($F = 6.09$, $p = 0.019$) as the smoothing functions were not statistically different among lakes ($F = 1.19$, $p = 0.284$). In contrast, both shallow lakes demonstrated similar average water transparency over the entire time period (lake effect: $F = 0.01$, $p = 0.933$; Figure 2d). Secchi depth significantly increased in the shallow reference lake over time ($F = 13.76$, $p < 0.001$), water transparency did not change appreciably over time in the fertilized shallow lake ($F = 28.91$, $p < 0.001$; Figure 2d). We observed no consistent trends in dissolved organic carbon across time in any of the lakes (Figure S2).

In the fertilized deep lake zooplankton appeared to respond to the increase in algal abundance from fertilization (Figure 2e). At the start of the study, zooplankton biomass was similar at ~100 μg L^{-1} in both deep lakes and was similar over the entire time period, on average ($F = 0.01$, $p = 0.932$; Table 2). Although zooplankton biomass did not change significantly over time in the reference deep lake ($F = 0.26$, $p = 0.654$), zooplankton biomass increased to a maximum of 184 μg L^{-1} in the fertilized deep lake in 2011, an 88% increase relative to the beginning of the study ($F = 3.97$, $p = 0.011$). Zooplankton biomass was on average nearly 3× higher in both shallow lakes compared to the deep lakes, and average biomass was not statistically different among shallow lakes ($F = 2.38$, $p = 0.132$). Zooplankton biomass declined over time in the reference shallow lake with only marginal statistical significance ($F = 3.84$, $p = 0.059$), and the declines were not different between the reference and fertilized shallow lakes ($F = 1.91$, $p = 0.167$; Figure 2f). In the fertilized

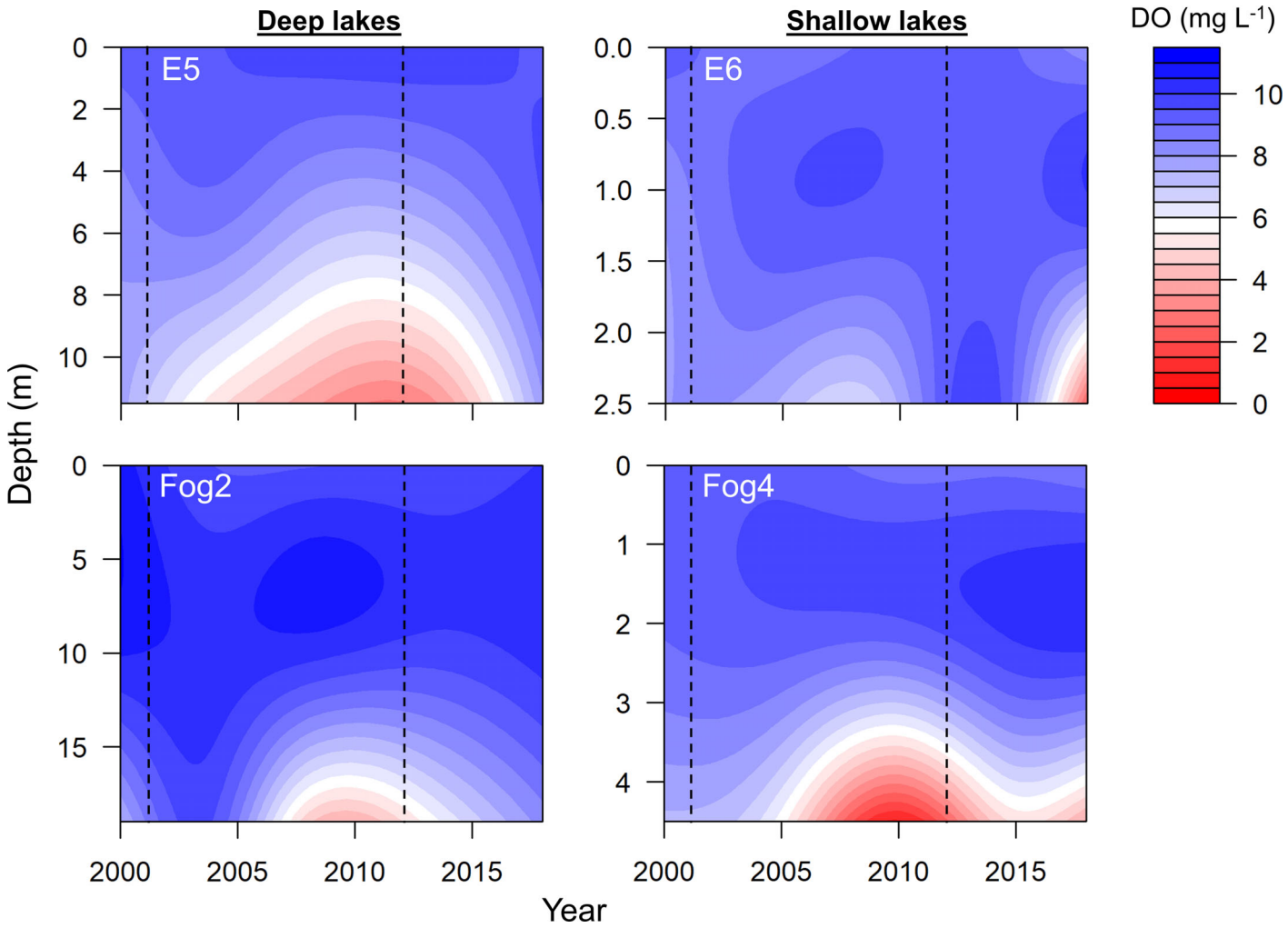

Figure 3. Filled contour plots of dissolved oxygen concentration (mg L^{-1}) from profiles measured in deep (E5, Fog2) and shallow (E6, Fog4) lakes in July over time. The dashed vertical lines indicate the start and end of the fertilization treatment. A natural thermokarst event was observed in lake Fog4 from 2002 to 2004. *Y*-axes scales differ among panels.

Table 3. Output from multivariate linear models for zooplankton biomass composition sampled from 2000 to 2018 in four arctic Alaskan lakes. Models were run separately for deep lakes (E5, Fog2) and shallow lakes (E6, Fog4) to quantify effects of time and fertilization on assemblage composition. Significant effects ($p < 0.05$), after correcting for multiple testing, are in bold. Percent of *Sum of-F* is displayed for species with significant relationships. Statistics were run on log-transformed data.

		F-statistic			Percent of *Sum-of-F*		
Lakes	Taxa	Year	Fertilization	Year × Fertilization	Year	Fertilization	Year × Fertilization
E5-Fog2	Global model	*13.19*	***304.4***	***42.79***			
	Bosmina	0.01	3.59	5.11			
	Cyclopoid	1.24	**19.69**	0.39		**6%**	
	Daphnia longiremus	0.01	**99.15**	2.60		**33%**	
	Daphnia middendorffiana	0.15	**80.23**	3.27		**26%**	
	Diaptomus	5.35	**7.64**	0.51		**3%**	
	Heterocope	2.44	**58.49**	**10.48**		**19%**	**25%**
	Holopedium	4.02	**35.57**	**20.43**		**12%**	**48%**
E6-Fog4	Global model	***59.22***	***112.2***	*12.56*			
	Bosmina	0.15	1.73	2.82			
	Cyclopoid	**12.67**	**14.65**	1.56	**21%**	**13%**	
	D. longiremus	**6.41**	0.01	0.05	**11%**		
	D. middendorffiana	**11.13**	0.02	<0.01	**19%**		
	Diaptomus	**14.28**	0.02	<0.01	**24%**		
	Heterocope	**13.17**	0.07	1.24	**22%**		
	Holopedium	1.42	**93.11**	4.25		**83%**	

shallow lake, zooplankton biomass declined after 2012 and remained <81 $\mu g\ L^{-1}$.

Hypolimnetic dissolved oxygen (DO) declined by 43% in the fertilized deep lake from 2002 to 2011 ($F = 7.11$, $p < 0.001$; Figure 2g). Conversely, DO in the reference deep lake varied between 10 and 13 $mg\ L^{-1}$ with no significant trend ($F = 1.48$, $p = 0.213$; Table 2). The reference deep lake had significantly higher DO on average than the fertilized lake ($F = 304.9$, $p < 0.001$). While the reference shallow lake exhibited higher average DO than the fertilized lake ($F = 4.63$, $p = 0.039$; Figure 2h), DO did not change significantly in the reference lake over time ($F = 1.94$, $p = 0.173$), and trends in DO over time did not differ among shallow lakes ($F = 0.19$, $p = 0.669$). Toward the end of the fertilization, we observed a dramatic increase in hypolimnetic anoxic conditions in both the fertilized deep lake and the reference shallow lake (Figure 3). In 2010, the fertilized deep lake was hypoxic (<4 $mg\ L^{-1}$) from nearly 8 m to the bottom, and the reference shallow lake was hypoxic from 3.5 m to the bottom. The reference deep lake also demonstrated a small zone of low oxygen in 2010, but only near the very bottom (18 m). The fertilized shallow lake only exhibited low oxygen conditions at the very end of the time series at depths >2 m (Figure 3).

Phytoplankton assemblage composition

Phytoplankton assemblage composition was variable over time with different taxa increasing or decreasing in relative abundance (Figure S1). Generally, composition was more consistent among years in the deep lakes (smaller shifts in ordination space) relative to the shallow lakes (Figure S1a). Notable changes to the phytoplankton community were detected after fertilization in the deep lake (2002 vs. 2012) and included an increase in representation by diatoms (Bacillariophyta) and golden-brown algae (Chrysophytes), and a significant proportion of euglenids (Euglenophyta) were detected (Figure S1b). Conversely, the fertilized shallow lake was highly dynamic with relatively large shifts in phytoplankton composition throughout the study (Figure S1a). Notable changes to the phytoplankton community after fertilization in the shallow lake included an increase in representation by cyanophytes and an increase in the proportion of diatoms (Bacillariophyta; Figure S1b).

Zooplankton assemblage composition

As with phytoplankton, zooplankton assemblages exhibited both temporal variation in composition and total biomass that differed among lakes. There was an interactive effect between time and fertilization at the assemblage-level for the pair of deep lakes ($F_{1,33} = 42.79$, $p < 0.001$; Table 3), which was driven by higher biomass of *Heterocope* and *Holopedium* in the fertilized lake relative to the reference lake from 2000 to 2009 and the decline of these two groups and all taxa generally after 2010 (left, Figure 4). As presented above, zooplankton biomass in the reference deep lake showed no decline over time. The effect of

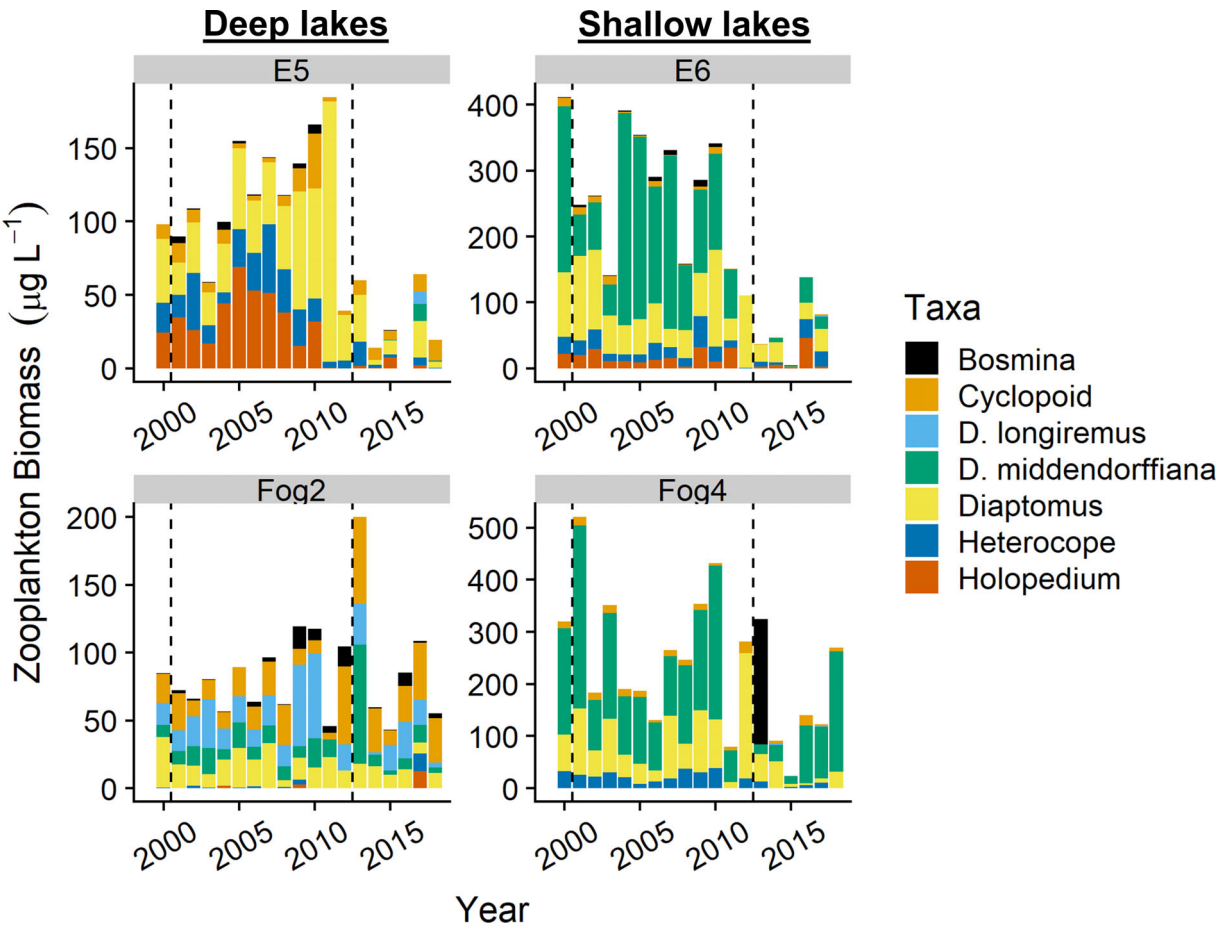

Figure 4. Zooplankton biomass composition in each of the four study lakes. Dashed vertical lines represent the start and end of fertilization in E5 and E6. Major taxa are shown in the legend. We observed a natural thermokarst event in lake Fog4 from 2002 to 2004.

Table 4. Model output from generalized additive models (GAM) for fish CPUE over time, relative condition over time, and relative condition as a function of CPUE. Lake was included as a parametric predictor in GAMs to account for differences in mean values between lakes. Lake was included as a parametric predictor to account for differences in mean values between lakes, and we treated lakes as ordered factors to test for differences in smoothing terms between paired lakes. Positive coefficient estimates mean the reference lake had higher values, on average. We used thin plate regression splines by lake to test for differences between smoothing functions of paired lakes. *F*-statistics and effective degrees of freedom (*edf*) are provided, and *p*-values <0.05 are shown in bold. The "Reference smooth" effect represents the smoothing term for the reference lake over time, while the "Fertilized vs. reference smooth" effect represents whether smoothing splines differ between the reference and fertilized lake in a pair.

Response	Effects	Coefficientestimate (SE)	*F*	*edf*	*p*	Devianceexplained (%)
Fish CPUE	Lake	−0.929 (0.187)	24.75	1	**<0.001**	63.9
	Reference smooth		4.89	4.36	**0.035**	
	Fertilized vs. reference smooth		3.53	1	**0.010**	
Relative condition	Lake	0.24 (0.01)	1257	1	**<0.001**	56.0
	Reference smooth		66.51	7.30	**<0.001**	
	Fertilized vs. reference smooth		51.38	7.59	**<0.001**	
Relative condition	Lake	0.19 (0.06)	11.25	1	**<0.001**	52.5
	Reference smooth		54.27	8.08	**<0.001**	
	Fertilized vs. reference smooth		23.33	8.14	**<0.001**	

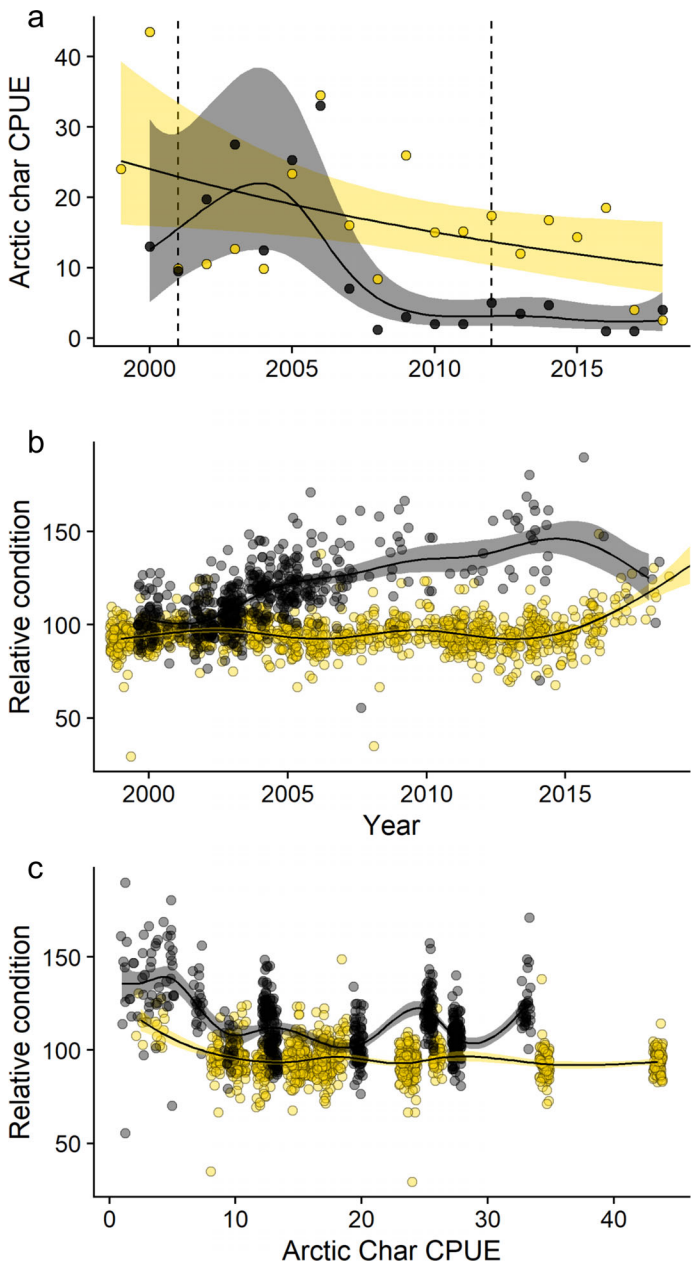

Figure 5. (**a**) Fish catch per unit effort (CPUE) over time in the fertilized deep lake (yellow) and reference lake (black). The dashed vertical lines indicate the start and end of the fertilization. (**b**) Fish relative condition increased on average over time in the reference deep lake, and remained relatively constant in the fertilized deep lake. (**c**) Fish relative condition increased in both lakes once CPUE was <10. Lines are smoothing splines with 95% confidence intervals from generalized additive models. Output from generalized additive models is presented in Table 4.

fertilization was also significant ($F_{1,34} = 304.4$; $p < 0.001$), which suggests differences in composition between the two deep lakes (Figure 4). Six taxa differed significantly in biomass between the deep lakes with the two *Daphnia* taxa contributing to 59% of assemblage-level differences between lakes (Table 3).

Zooplankton composition in the shallow lakes also exhibited significant effects of year ($F_{1,35} = 59.22$, $p = 0.002$) and fertilization ($F_{1,34} = 176.7$, $p = 0.002$; Table 3). The absence of *Holopedium* contributed to 83% of the assemblage-level differences between shallow lakes (fertilization effect; Table 3). Five of the seven taxa contributed to the significant year effect, explaining 97% of the assemblage-level variation over time (Table 3; Figure 4). Unlike in the deep lakes, there was no significant interactive effect of time or fertilization in the shallow lakes ($F_{1,33} = 12.56$, $p = 0.107$; Table 3).

Fish CPUE and condition

As with zooplankton, char abundance and condition responded differently over time between the deep fertilized and reference lakes (Table 4). The fertilized lake had higher CPUE relative to the reference lake ($F = 24.75$, $p < 0.001$), and responses among lakes differed over time ($F = 3.53$, $p = 0.010$; Figure 5a). Catch per unit effort in the fertilized lake steadily declined on average, but was stochastic with decreases and increases over time before stabilizing around 2010. However, by 2017 CPUE had declined to values similar to the reference lake (Figure 5a). The reference deep lake demonstrated initial increases in CPUE from 2000 to 2006, but then declined to low levels (<10), and remained low for the rest of the study. There were gradual changes in fish total length in the fertilized deep lake across the study (Figure S2); however, fish size in the reference deep lake increased dramatically after 2006, peaked in 2013, and declined to values similar to those in the fertilized lake by 2018 ($F = 16.28$, $p < 0.001$) Fish condition was significantly higher, on average, in the reference lake ($F = 1277$, $p < 0.001$; Table 4), and responses of fish condition over time were different among lakes ($F = 90.32$, $p < 0.001$). Condition in the reference deep lake increased over time before stabilizing after 2010 (Figure 5b). In the fertilized deep lake, fish condition was relatively constant for much of the study period (1999–2016) before increasing once CPUE declined in the last years of the study, at which point every fish was in above-average condition (Relative condition >100; Figure 5b). Higher fish condition, on average, in both lakes coincided with CPUE <10 (Figure 5c).

Discussion

Timescale and nonlinearity of responses

Experimental fertilization studies show how nutrient limitation determines ecosystem function and structure (e.g., Elser et al. 2001). These experiments are even more relevant in the Anthropocene, given interactions between direct and indirect effects of climate change, specifically nutrient enrichment (*this study*, Porter et al. 2013). Arctic lakes, in a region where the climate is changing most rapidly, may be especially sensitive to nutrient-related disturbance; however, some effects can be slow and subtle. In this study, we report on a low-intensity fertilization experiment meant to mimic the response of lakes of differing morphometry (deep, shallow) and with and

without fish to the indirect effects of climate change via nutrient delivery from increased weathering or thermokarst failures in the catchment. We hypothesized lake morphometry and the presence of fish would modify the responses to fertilization due to differences in the relative contribution of benthic vs. pelagic processes and predation on zooplankton, respectively, and both the fertilization response and recovery would be more rapid at lower trophic levels and lagged at higher trophic levels. In the fertilized deep lake with fish, there was a significant response to fertilization at all pelagic trophic levels. However, many of the observed patterns were slow to emerge and nonlinear, perhaps indicating certain thresholds needed to be met to stimulate a response at the next trophic level (e.g., Carpenter et al. 2001). The overall response took more than 10 yr to be fully expressed in most response variables in our experimental lakes, indicating some degree of resistance to change. During the recovery period, however, some response variables had relatively high resilience and returned rapidly to preperturbation levels (e.g., chl *a*) while others such as zooplankton and fish remained in very altered states up to 6 yr after the fertilization was terminated. Although we had limited premanipulation data and could not control for natural variability in local weather or lake characteristics, relative to the reference lakes the responses to fertilization were strong and the patterns were largely evident.

The effect of morphometry and fish presence

As predicted, the lake ecosystem response to fertilization varied among deep lakes with fish and shallow fishless lakes. In deep lakes with fish, fertilization generally caused direct stimulation of the pelagic food web initially via a strong bottom-up effect from nutrients to phytoplankton to zooplankton to fish. Productivity in ice-free arctic lakes of this region is nutrient limited, so the large overall increase in chl *a* we observed after fertilization in the deep lake is somewhat predictable. Previous arctic lake fertilizations resulted in a phytoplankton response to increased N alone and to P alone (Luecke et al. 2014), and to N and P together (Levine and Whalen 2001). Our results suggest positive responses to N and P addition based on the very large increase (201% between 2001 and 2012) in chl *a* (cf. Lewis and Wurtsbaugh 2008; Harpole et al. 2011; Lueke et al. 2014). Unsurprisingly, water transparency declined dramatically in the fertilized deep lake in response to the increase in chl *a* (Luecke et al. 2014), but not to a degree to which visual foraging effectiveness of fishes could be limited (van Dorst et al. 2019, 2020).

In contrast to the predicted effects of fertilization on the deep lake, we observed high natural variability and an inconsistent fertilization effect in the shallow lake relative to the start of the experiment or to the reference lake. This lesser effect in the shallow lake is in part because benthic primary production is predominant but is weakly affected by fertilization, because benthic algae are light limited in these lakes (Daniels et al. 2015). In addition, a thermokarst failure occurred naturally from 2002 to 2004 in the reference shallow lake, confounding our analysis but also offering an opportunity to measure the shallow lake response to thermokarst directly and compare to our attempts to mimic thermokarst impacts experimentally.

Overall, the thermokarst and fertilized responses were similar in the shallow lakes, with two main differences (statistically significant). The first main difference between the lakes was higher chl *a* in the reference lake at the start of the experiment and during the time of thermokarst activity. As the thermokarst activity subsided in the reference lake, levels of chl *a* returned to those observed in the fertilized lake for the remainder of the experiment. We interpret this to indicate initially higher nutrient additions to the reference lake from the thermokarst failure than were added experimentally to the fertilized lake, and while strong thermokarst activity (slumping of material into the lake) declined after 2004, dissolved nutrient inputs may have continued. An alternative explanation is that differential grazing pressure from large-bodied cladoceran zooplankton, abundant in the shallow lakes without fish and known to reduce mid-summer algal biomass and productivity in these lakes, could have caused the observed differences in chl *a*. However, at the start and for most of the experiment the zooplankton biomass was similar between the fertilized and reference shallow lakes. The second main difference in response between the fertilized shallow lake and the reference shallow lake impacted by the thermokarst failure was the higher water transparency during the recovery period for the reference lake. This lower light attenuation in the reference lake was not caused by lower chl *a* levels relative to the fertilized lake, because chl *a* levels were similar in the two lakes during the recovery period.

Phytoplankton community changes

Changes in phytoplankton assemblages in treatment lakes were dramatic based on the available data (notably less available relative to other metrics and also asymmetric across time). After fertilization (2012), we observed an apparent increase in the proportion of diatoms, golden-brown algae, and euglenids in the fertilized deep lake. Notably these taxa also increased in nutrient enrichment experiments in other subarctic lakes (Holmgren 1984; O'Brien et al. 1992). The euglenids were mixotrophic flagellates that tend to prefer higher productivity aquatic ecosystems (O'Brien et al. 1992). Similarly, the phytoplankton community in both shallow lakes appeared to demonstrate large changes in composition across years, likely due to both fertilization and thermokarst activity. In both shallow lakes, we observed an increase in cyanophytes and in diatoms in the reference shallow lake. With an increase in available phosphorous, the proportion of cyanophytes increased after fertilization, even with the added N from fertilization. The dominant cyanophytes (*Pseudanabaena*) were large-bodied and experience little top-down grazing control from herbivorous zooplankton (Davidowicz et al. 1988). Cyanophytes tend to

dominate under higher nutrient concentrations and lower light levels as observed in other fertilized or more eutrophic lakes (e.g., Taranu et al. 2015). The direct effects of climate change such as lake warming and changes to lake thermal regimes and indirect effects such as increased nutrient loading are all predicted to increase the dominance of cyanophytes in lakes (Wagner and Adrian 2009; Elliot 2012).

Zooplankton response

The presence of fish has large top-down effects on zooplankton abundance, diversity, and body size in arctic lakes (Luecke et al. 2014). Thus, the delayed response of zooplankton to nutrient additions in the deep fertilized lake could suggest fish readily consumed more zooplankton as they were produced, limiting an immediate response in resource availability. However, once chl *a* exceeded 5 $\mu g\ L^{-1}$ (after ~5 yr) and before fish abundance increased, zooplankton biomass increased to extremely high levels. Later in the time series in the fertilized deep lake, zooplankton populations collapsed and never recovered. Predation by char may have caused this collapse, suggesting that control of zooplankton may have shifted between resource availability at the beginning of fertilization to consumption by predators toward the end of fertilization (cf. Carpenter and Kitchell 1996; Rogers et al. 2020). In previous high-nutrient lake fertilization experiments on the North Slope, similar lags were observed with different zooplankton taxa reacting at different time periods in part due to an interaction with temperature (Kling 1994; Luecke et al. 2014). As such, much of the remaining variation in zooplankton density across years in the Arctic and observed here is likely due in part to an interaction with temperature, where warmer years lead to greater zooplankton density and biomass (Klobucar et al. 2018). Although we observed no substantial trends in lake temperature during our experiment (Figure S4), these observations highlight the need to explicitly consider abiotic effects of temperature on ectotherms when evaluating the indirect (nontemperature) effects of climate change (see also Klobucar et al. 2018).

In addition to large changes to zooplankton biomass in the fertilized deep lake relative to prefertilization and to the reference deep lake, we also observed changes to the zooplankton community over time. A large portion of the community change and the response to fertilization is attributed to a significant decline in *Holopedium* and *Heterocope* in the fertilized deep lake starting late in the fertilization period (2012). The declines in *Holopedium* and *Heterocope* appear to be in response to the increase in the relative abundance (CPUE) of fish, a factor which strongly controls zooplankton abundance across fish and fishless lakes (Hershey et al. 1999; Johnson et al. 2010; Luecke et al. 2014). *Holopedium* also rarely occurs in nutrient enriched lakes and appear to be oligotrophic obligates (Hessen et al. 1995). And while their gelatinous sheath may aid in avoiding predation to some degree, they can be readily consumed by fish, neonate predation can be high, and fish density controls their abundance (e.g., Stenson 1973; Tessier 1986). In the Arctic, *Heterocope* is a large-bodied zooplankter strongly preferred by fish (O'Brien et al. 2004; Luecke et al. 2014). Zooplankton biomass in the shallow lakes did not increase in response to fertilization, either because zooplankton in these shallow lakes are less food limited or because the thermokarst effect on the reference shallow lake masked a fertilization response, or most likely, some combination of both. The much greater biomass of zooplankton overall in shallow lakes vs. deep lakes is common in the Arctic and is due to the lack of fish predation (Luecke et al. 2014). In sum, the observed switch to a strong top-down effect of fish on zooplankton in the fertilized deep lake is likely responsible for some of the nonlinear dynamics we observed in response to fertilization, which prevailed throughout the recovery period to the end of the study.

Fish response

The response of lower trophic levels translated to an intriguing response at the highest trophic level, fish. Arctic char catch-per-unit-effort (CPUE) reached the highest values in the latter half of the fertilization period. In previous fertilization experiments, it similarly took shorter-lived fish at least 3 yr to incorporate the new energy supply (Lienesch et al. 2005; Luecke et al. 2014). We observed relatively high char CPUE in 2005, 2006, and 2009 after zooplankton biomass had increased to highs of 150 $\mu g\ L^{-1}$, several orders of magnitude higher than observed previously in these arctic lakes (Luecke et al. 2014). At that point high char numbers appear to have collapsed the zooplankton population via predation. Subsequently, char CPUE declined to low levels and remained low until the end of the time series. Lienesch et al. (2005) similarly observed an increase in growth rates of lake trout during fertilization and a rapid decline postfertilization. We have frequently observed similar relationships between high fish density and low zooplankton abundance and species diversity in other unperturbed ARC LTER char lakes (Luecke et al. 2014). Arctic char are extremely omnivorous in these lakes with little connectivity to streams or other lakes, and they opportunistically consume a diverse diet. They do consume a significant portion of benthic invertebrates, which were not considered as part of the pelagic response described in this study; however, their diet can be dominated by zooplankton, especially when fish are smaller (Luecke et al. 2014; Klobucar and Budy 2020). As such, char could quickly respond to the increase in zooplankton food availability with likely greater recruitment success. Char CPUE in the reference deep lake was relatively low throughout this study on average, and zooplankton biomass composition was correspondingly stable and relatively speciose throughout the time series. Accordingly, fish condition (and size in the reference deep lake) increased dramatically with large declines in CPUE in both deep lakes; strong cycles in size structure are common in these closed lakes (Budy and Luecke 2014). The

observed patterns herein reinforce that these lakes are sensitive to density dependent population regulation, as has been demonstrated elsewhere (e.g., Amundsen et al. 2007; Budy and Luecke 2014). The presence or absence of fish and lake morphometry are two of the most influential factors determining the biology of arctic lakes, as highlighted above (Hershey et al. 1999; Johnson et al. 2010).

The response of fishes to nutrient addition also depends on habitat conditions. The hypolimnion of some smaller arctic lakes is naturally hypoxic for at least part of the summer (Luecke et al. 2014), and thus unavailable to fish. With an increase in nutrients, we observed a dramatic decline in hypolimnetic (<8 m) DO concentrations in the fertilized deep lake. Oxygen was particularly low in August and below the minimum of 5 mg L^{-1} required for fish respiration. Luecke et al. (2014) similarly observed oxygen concentrations <5 mg L^{-1} toward the end of a heavy fertilization experiment in a nearby arctic lake; those low-oxygen conditions persisted for at least 7 yr post-fertilization. Near the end of our fertilization, the hypoxic zone in the hypolimnion of the fertilized deep lake expanded such that char lost approximately 12% of their available habitat. A reduction in habitat of that magnitude could exacerbate already strong density-dependent regulation and result in metabolic stress and more energy required from food (Budy and Luecke 2014). Furthermore, this loss does not account for habitat limitations in the epilimnion due to warmer epilimnetic water temperatures and a potential habitat squeeze (Hobbie et al. 1999; Ficke et al. 2007; Budy et al. 2009). Interestingly, Caldwell et al. (2020) recently demonstrated that although the littoral zone experienced greater production with earlier ice-off in Castle Lake, California, U.S.A., trout did not use the increased littoral production because littoral temperatures were too warm. These secondary and complex effects of climate change, whether direct or indirect effects, are difficult to predict but can be extremely influential on biotic responses (Pennock et al. 2021). The combination of increased eutrophication and increased temperature may be devastating to native fishes in these small arctic lakes.

Ecological resistance

We observed multitrophic-level bottom-up and top-down responses to our whole-lake nutrient addition experiment, with various resistance and resilience to change and return times after disturbance. Bottom-up increases in chl *a* and decreases in hypolimnetic oxygen were more rapid than the response of higher trophic levels, as expected, but there was some resistance to change even in DO and chl *a*, which had time lags of one to several years. Resistance to disturbance from anthropogenic or experimental nutrient inputs to arctic lakes can be very low (i.e., an immediate response; Schindler 1974; Lienesch et al. 2005; O'Brien et al. 2005) or moderate, with response lags of two to many years (Welch et al. 1989; Michelutti et al. 2007; Stewart et al. 2018). The cause of such muted responses is thought to be related to the extreme environment and long ice cover in arctic lakes (Douglas and Smol 2000; Stewart et al. 2018), although we note here that the strength of nutrient addition is also likely important. For example, low resistance occurs with strong, experimental, or anthropogenic additions (Schindler 1974; O'Brien et al. 2005; Lienesch et al. 2005), while moderate resistance is observed with lower-level fertilization (this study; Welch et al. 1989; Michelutti et al. 2007; Stewart et al. 2018).

Higher trophic levels showed more resistance to disturbance, and there was a time lag of at least several years before top-down responses occurred (e.g., fish predation on zooplankton), again as we expected. Once they occurred, these strong top-down ecological interactions resulted in several trophic groups switching from a positive response to a negative response to fertilization. The response of zooplankton to fertilization was at first positive and significant, but then ultimately negative due to intense fish predation. Such trophic interactions are often found in studies of top-down manipulations of food webs (e.g., Carpenter and Kitchell 1996), and here we show that similar effects can occur after many years with low-level nutrient fertilization.

Recovery from fertilization

Return time is the time period necessary for a system to return to a particular configuration after disturbance, and it is related to resilience (May 1974; Carpenter and Cottingham 1997). The return times of different variables after the termination of fertilization in the recovery period we monitored were more rapid at lower trophic levels, as predicted. Chlorophyll *a*, for example, remained high the first year after fertilization but by year 3 dropped substantially and had returned to prefertilization levels by year 4. This rapid return time for chl *a* of ~3–4 yr is similar to that observed in fertilization studies of other arctic lakes (Kling 1994; Lienesch et al. 2005; O'Brien et al. 2005) and in temperate-zone lakes after anthropogenic nutrient inputs are reduced (e.g., Edmonson 1991; Ibelings et al. 2007). @@@Similarly, DO increased substantially by years 2 and 3 in the recovery period, and returned to prefertilization levels by years 4 to 5. This return time was more rapid than that observed in two other arctic lake fertilization studies, where DO remained low in hypolimnetic waters for at least 4–6 yr (Lienesch et al. 2005; O'Brien et al. 2005). However, both of those experiments used high nutrient addition, 4–5 times higher than background loading, whereas our low-level fertilization was only 2–3 times background, and thus we interpret our lower nutrient inputs to result in shorter return times.

In contrast, zooplankton biomass and fish abundance remained at historic lows throughout the recovery period, and thus had return times of greater than 6 yr (the length of our recovery monitoring). The loss of habitat during the fertilization due to hypoxia was one of the more dramatic impacts, for fishes in particular, and a contributor to the long-return time. Arctic fishes are slow-growing and long-lived, and major die-offs from hypoxia or extreme conditions in 1 yr could take

more than a decade for full population recovery, assuming only partial mortality. Although DO had increased to near pretreatment values just 3 yr into the recovery, the char population was still greatly reduced, likely partially in response to several years of hypoxia. Such sensitivity to disturbance is seen in other lakes, and can lead to state-space changes (reviewed in Carpenter et al. 2001). From that standpoint, arctic lakes may be more sensitive than lakes in other regions, to the direct and indirect effects of climate change, even if the resulting nutrient enrichment is at a relatively low level.

The recovery or return time of lake ecosystems from nutrient enrichment varies with trophic level (e.g., Knapp et al. 2001; Shade et al. 2012; McCrackin et al. 2017), and lakes with longer food chains typically have longer return times than do lakes with shorter food chains (Pimm and Lawton 1977; Carpenter et al. 1992). In addition, a recent meta-analysis showed that on average the recovery from eutrophication in lakes and coastal ecosystems took years to decades, for all trophic levels (McCrackin et al. 2017). While arctic lake ecosystems are initially resistant to low-level nutrient increases, over the long term they have low resiliency and are slow to return to their initial state, similar to lake ecosystems at lower latitudes. Our results show that low-level nutrient additions from the indirect effects of climate change can have substantial, long-term effects on lake ecosystems.

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Conflict of interest

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